J. Anat. (1984), **138**, 1, pp. 55–65
With 11 *figures*
Printed in Great Britain

The anatomy and histology of the nasal cavity of the koala (*Phascolarctos cinereus*)

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(*Accepted* 5 *May* 1983)

INTRODUCTION

The fine structure of olfactory and vomeronasal chemosensory epithelium has been investigated in many mammals, revealing a uniform pattern with only minor species variation (Graziadei, 1977). Fewer studies have been done on the respiratory epithelium (Adams & McFarland, 1972; Matulionis & Parks, 1973; Kratzing, 1982*a*), the structure and distribution of nasal glands (Bojsen-Møller, 1964; Adams, 1982), and the general anatomy of the nose (Negus, 1958; Parsons, 1971; Stoddart, 1980). Yet these may all vary with the feeding patterns of the animal, the need to conserve moisture, and the provision of temperature control for inspired air or, in some cases, cooling mechanisms for the vascular supply to the brain. A continuing study of the olfactory and vomeronasal organs in Australian marsupials suggests that variations occur in nasal architecture to serve specific needs. The nose of the koala has been investigated as part of this study and reveals some features which may be related to its highly specialised diet, nocturnal habits, and known ability to conserve water.

MATERIALS AND METHODS

Specimens were obtained from three healthy young adult males and one older female that had suffered accidental injuries and had poor prospects for recovery, and one pouch young too small to survive maternal death. For electron microscopy, tissues were fixed by perfusion with glutaraldehyde under terminal anaesthesia, as previously described (Kratzing, 1982*a*). Tissues for light microscopy were taken from the same specimen at the same locations in the opposite side of the nasal cavity. Tissues for light microscopy from other specimens were fixed by immersion in 10 % formaldehyde and decalcified in ethylenediaminetetraacetic acid (EDTA); both sets of tissues were embedded in paraffin, sectioned at a thickness of 6 μm and stained with haematoxylin and eosin, alcian blue or periodic acid–Schiff. The head of the young specimen was fixed in formalin, decalcified in formic acid, embedded in paraffin and serially sectioned at a thickness of 7 μm. Every tenth section was mounted and stained with haematoxylin and eosin, and representative sections were stained with alcian blue and periodic acid–Schiff.

To study the gross anatomy of the nose, a fresh unfixed head was deep-frozen and sectioned transversely with a bandsaw into slices approximately 0·5 cm thick. These were fixed flat in 10 % formalin, photographed, and examined under a dissecting microscope to prepare diagrams of the nasal cavity and paranasal air sinuses.

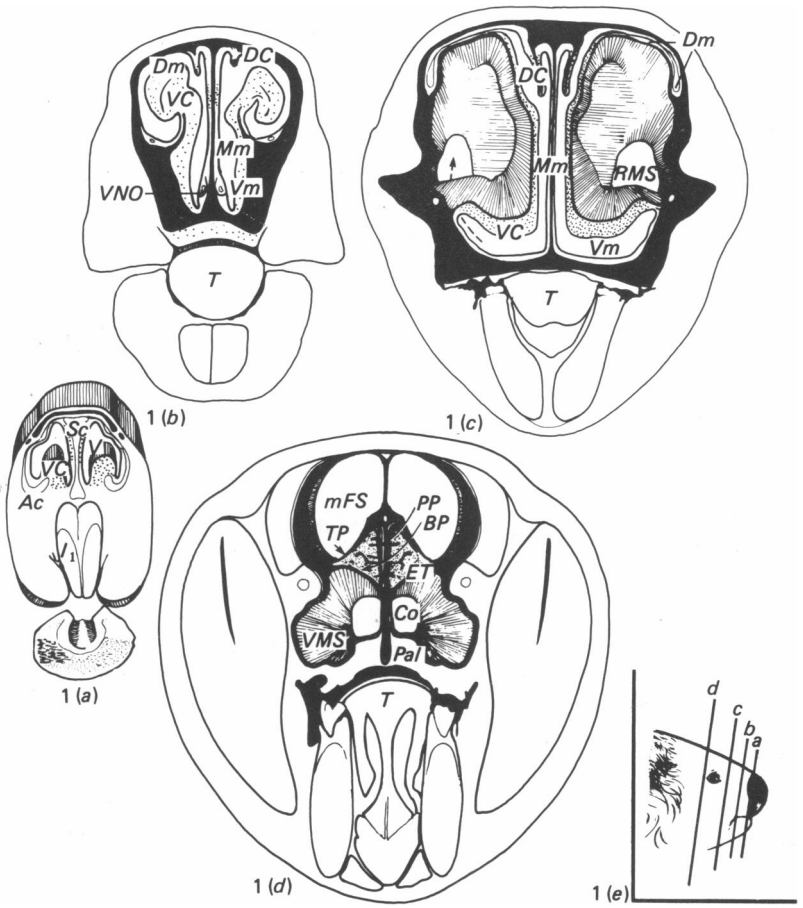


Fig. 1 (*a–e*). Diagrammatic thick (0·5 cm) transverse sections of the head of a koala. The position of each section is indicated in Fig. 1 *e*. *Ac*, alar cartilage; *BP*, basal plate (ethmoid); *Co*, choana; *DC*, dorsal concha; *Dm*, dorsal meatus; *ET*, ethmoturbinates; I_1, first incisor; *mFS*, medial frontal sinus; *Mm*, middle meatus; *PP*, perpendicular plate (ethmoid); *Pal*, perpendicular plate (palatine); *RMS*, rostral maxillary sinus; *Sc*, septal cartilage; *T*, tongue; *TP*, tectal plate (ethmoid); *V*, nasal vestibule; *VC*, ventral concha; *Vm*, ventral meatus; *VMS*, ventrocaudal maxillary sinus; *VNO*, vomeronasal organ.

RESULTS

Gross anatomy

The right and left nasal cavities were separate compartments as far back as the choanae, divided by a thin nasal septum. In rostral to caudal sequence, each had a vestibular area (Fig. 1 *a*), followed by the nasal cavity proper where the ventral and dorsal conchae formed a ventral, middle, and dorsal meatus (Fig. 1 *b*, *c*), and a caudal region where the ventral meatus was completely separated from the ethmoturbinate region (Fig. 1 *d*). The ventral meatus communicated with extensive paranasal air sinuses in the maxillary and frontal bones. There were two separate maxillary air sinuses: a rostral maxillary sinus which communicated with the nasal cavity via a restricted opening ventral to the attachment of the ventral concha to the lateral nasal wall, and a ventrocaudal maxillary sinus which communicated widely with the ventral meatus close to the choanae. Of the two frontal air sinuses, only one

was in communication with the nasal cavity since it was continuous with the rostral maxillary sinus. Together these sinuses encroached on the nasal cavity proper, so that the middle and dorsal meati were reduced to narrow slits (Fig. 1*b*, *c*).

Much of the space in the rostral nasal cavity was occupied by the large ventral concha. This began in the vestibule as a vascular and glandular ridge, supported by the curved end of the alar cartilage. Beyond the vestibule, cartilage was replaced by a simple curved plate of bone whose line of attachment to the lateral wall ran dorsally at the opening of the maxillary sinus. Further caudally, the free margin of the concha curved dorsolaterally to attach to the lateral wall and enclose a conchal sinus.

The dorsal concha was a simple elongated bony plate covered by vascular mucosa. It extended down a short distance from the roof of the nasal cavity lying almost parallel with the septum, but curved slightly to accommodate the dorsal extent of the ventral concha. The nasal septum in the main part of the cavity was also a thin plate of bone covered by glandular mucosa, gradually replaced dorsoventrally by olfactory epithelium (Fig. 1*c*, *d*). There were no expansions of the septum to form 'swell bodies', but in the rostral part of the cavity the base of the septum extended to accommodate the vomeronasal organ and an extensive glandular area (Fig. 1*b*).

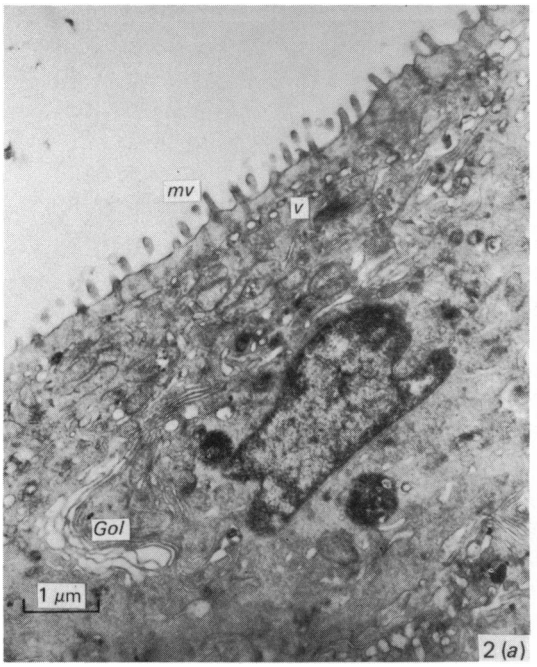
The nasal and oral cavities communicated via patent incisive ducts. The oral opening of each duct lay lateral to the incisive papilla on the rostral palate, and the duct sloped dorsocaudally to open into the nasal cavity at about the level of the fourth incisor, just rostral to the opening of the vomeronasal ducts. The tubes of the vomeronasal organ lay on either side of the septum, surrounded by curved cartilages. The lumen of the organ ended just rostral to the first cheek tooth, but the glands associated with it extended further caudally.

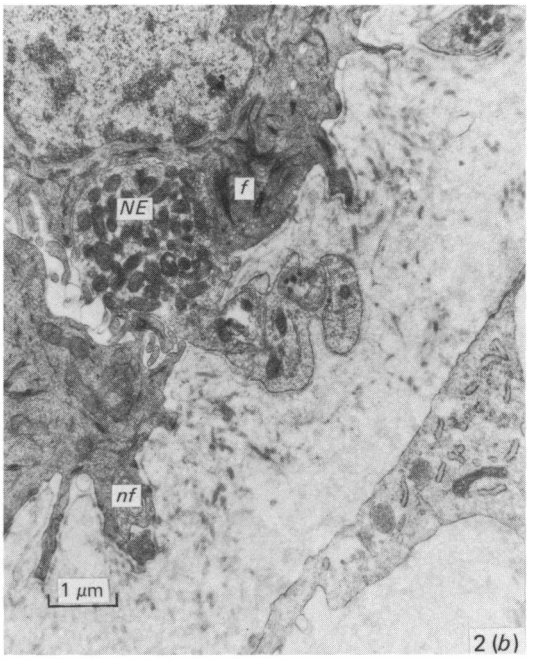
The ethmoidal region at the caudal extremity of the middle meatus consisted of four endoturbinate bones and a smaller ectoturbinate bone on each side of the perpendicular plate (Fig. 1*d*). Thin base plates shut off the region from the main air passage in the ventral meatus. Dorsally, the ethmoturbinate bones were separated by tectorial plates from paired medial frontal sinuses. The latter did not appear to communicate with the nasal cavity.

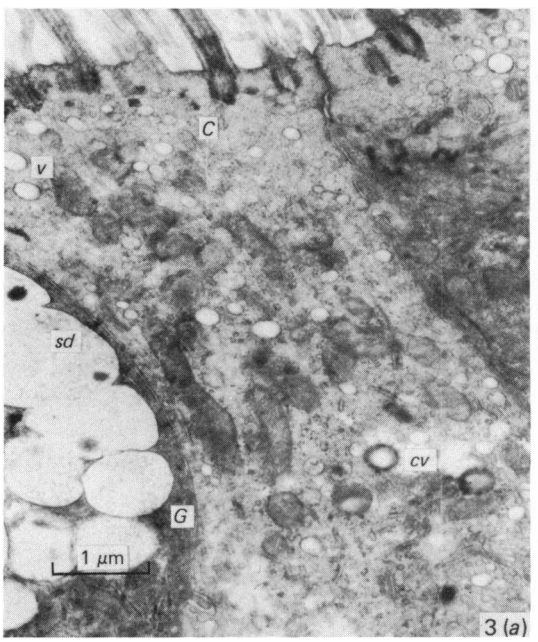
Histology

The vestibule was lined by low stratified squamous epithelium which was gradually replaced from the roof ventrally by ciliated pseudostratified epithelium. Similar squamous epithelium lined the terminal part of the nasolacrimal duct and the incisive duct, and consisted of three to four cell layers. The surface cells carried short microvilli and contained many clear cytoplasmic vesicles. Basal cells had many fibrillar bundles and irregular basal processes extending into the underlying connective tissue, giving the visual appearance of a root system (Fig. 2*a*, *b*). In some regions, these projections were closely associated with nerve endings.

The opening of the incisive duct marked the furthest extension of squamous epithelium into the nasal cavity proper. The maxillary sinus and most of the main cavity were covered by respiratory epithelium formed by basal, secretory (goblet) and ciliated cells. There was some regional variation in epithelial height and in goblet cell distribution. These cells constituted about one third of the surface cells on the septum, rostral ventral turbinate and ventrolateral wall, but were infrequent in the maxillary sinus. Ciliated cells had clear vesicles in their apical cytoplasm resembling those in surface cells of the vestibular epithelium, and the basal cells of both epithelia were very similar (Fig. 3*a*, *b*).







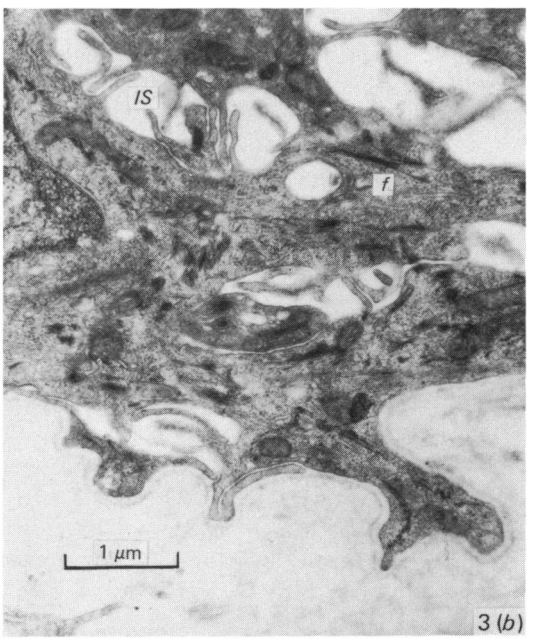


Fig. 2(*a–b*). Surface (Fig. 2*a*) and base (Fig. 2*b*) of vestibular epithelium from the ventral nasal floor near the opening of the nasopalatine duct. Surface cells have short microvilli (*mv*), numerous clear vesicles (*v*), and a prominent Golgi apparatus (*Gol*). Basal cell cytoplasm has numerous fibrillar bundles (*f*). Basal projections of these cells are associated with small nerve fibres (*nf*) and an expanded nerve ending (*NE*) with numerous mitochondria.

Fig. 3(*a–b*). Surface (Fig. 3*a*) and base (Fig. 3*b*) of respiratory epithelium from the nasal septum. Ciliated cells (*C*) have numerous clear vesicles (*v*) and some coated vesicles (*cv*). Secretion droplets (*sd*) in goblet cells (*G*) have contents of variable density. At the base of the epithelium there are wide intercellular spaces (*IS*). Basal cells have dense cytoplasm with fibrillar bundles (*f*) and irregular basal projections.

There was considerable variation in the lamina propria under different areas of respiratory epithelium. Over the ventral turbinate bone it was highly vascular; the vessels had thick muscular walls facing the conchal bone changing abruptly to thin superficial walls under the epithelium. In the vestibular part of the ventral concha, the vessels were supported by a network of fibrous trabeculae. Glands occurred in isolated patches in the conchal lamina propria; their cells had abundant granular endoplasmic reticulum and apical secretion granules of very variable density. The lateral borders of the cells extended into numerous fine projections (Fig. 4*a*). The glands opened to the turbinate surface via striated ducts.

The mucosa on the dorsal concha was less vascular. Its glands lacked striated ducts, but alveoli and ducts were surrounded by myoepithelial cells (Fig. 4*b*). The scattered glands in most of the septum resembled those of the dorsal concha, but the ventral septum had numerous glands which did not have myoepithelial cells and which discharged via short ducts with cuboidal lining (Fig. 5). This area was highly vascular, with thin-walled sinusoidal vessels.

Olfactory epithelium covered the ethmoturbinate area and much of the caudal part of the dorsal concha and septum. It conformed to the general pattern of mammalian olfactory epithelium and consisted of sensory and supporting cells and a thin line of basal cells. Supporting cells formed a thick surface fringe of microvilli which surrounded the ciliated olfactory rods on the sensory cells (Fig. 6). Supporting cells had extensive whorls of smooth endoplasmic reticulum in their apical cytoplasm and an occasional basal body.

Lamina propria under the olfactory epithelium was occupied by simple tubular olfactory (Bowman's) glands. Like the goblet cells of the respiratory epithelium, their secretion stained with periodic acid–Schiff and with alcian blue. Secretory cells had abundant granular endoplasmic reticulum, mitochondria, and pale secretion droplets (Fig. 7).

The vomeronasal organ was lined medially by sensory epithelium, and laterally by ciliated epithelium. Vomeronasal sensory epithelium resembled olfactory epithelium in the arrangement of sensory, supporting and basal cells. Sensory cells had surface macrovilli, clusters of dark granules and basal bodies, but no cilia (Fig. 8). Their perikarya contained extensive parallel rows of granular endoplasmic reticulum and a well developed Golgi apparatus (Fig. 10). Supporting cells had finely fibrillar cytoplasm with tubular profiles of smooth endoplasmic reticulum. There were fewer but wider surface microvilli than on sensory cells. The pseudostratified ciliated epithelium of the lateral aspect of the vomeronasal organ had ciliated and non-ciliated cells in about equal numbers but no goblet cells (Fig. 9). Non-ciliated cells were more electron-dense, had parallel rows of granular endoplasmic reticulum, their cisternae sometimes dilated by an amorphous material of low electron density, and a laterally placed Golgi apparatus. Basal cells lacked the prominent fibrillar bundles seen in their counterpart in the respiratory epithelium.

The vomeronasal glands lay in the lamina propria dorsolateral to the lumen of the organ. They were long compound tubular glands which opened at the dorsal and ventral junctions of the sensory and non-sensory epithelium. Secretory cells had dark cytoplasm with several areas of Golgi membranes, and dark apical secretion granules (Fig. 11). Cells were grouped around a wide lumen and, except at the luminal surface, their lateral borders were widely separated, with fine cytoplasmic projections occupying the intercellular space. Duct cells resembled secretory cells but lacked secretion granules.

DISCUSSION

The most distinctive features of the nasal anatomy of the koala are its restricted size, the simple structure of the conchae, and relatively poor glandular development. The nasal cavity is much smaller than is suggested by the appearance of the animal or shape of its skull. Much of the air space of the head lies in the extensive maxillary and frontal sinuses, and is not exposed to constant air flow. There are no glands under the sinus epithelium and sparse goblet cells provide the only secretion. In most mammals studied, including marsupials, tubular sinus glands are located dorsally in the maxillary sinus and the lateral nasal gland extends into the ventral sinus area. This latter gland has not been found in any of the sections of adult koalas studied. However, in serial sections of the pouch-young specimen its duct is seen in the lateral wall dorsal to the ventral concha, ending in a small area of glandular alveoli. The gland, when present, opens into the vestibule close to the nasolacrimal duct and contributes significantly to maintenance of a moist nasolabial area (Bojsen-Møller, 1964). It is well developed in the bandicoot (*Isoodon macrourus*) and the honey possum (*Tarsipes rostratus*) (Kratzing, 1982*b*). Its absence in the adult koala may contribute to water conservation, since the koala seldom drinks and usually relies on its leafy diet for fluid intake.

The absence of 'swell bodies' on the septum is unusual. These symmetrical structures are present in many mammals and are believed to direct the main air flow to the left or right nasal passage by alterations in their vascularity (Bojsen-Møller & Fahrenkrug, 1971). They are usually the site of extensive glands, with one or more major ducts opening on their apex to humidify inspired air. In the koala their absence may be further evidence of fluid conservation but may also be related to the small volume of air reaching the middle and dorsal meati. The only large glandular area on the septum lies rostroventrally, superficial to the vomeronasal glands, with the ducts opening towards the highly vascular ventral concha. Since the structure of the conchal vessels suggests an ability to make rapid changes in mucosal thickness, this area may be able to achieve the alterations of air flow and humidification usually controlled by the swell bodies.

The simple structure of the conchae contrasts with the complex scrolled turbinate anatomy of many mammals (Negus, 1958). Turbinate vascular mucosa is considered to provide temperature control for inspired air, and in some species provides a cooling mechanism for blood subsequently flowing to the cranial cavity. Such needs may require only a relatively small turbinate area in an arboreal animal of nocturnal habits. Greatest vascularity occurs in the ventral concha, but there are venous sinuses under the respiratory epithelium of the septum and dorsal concha. Together with

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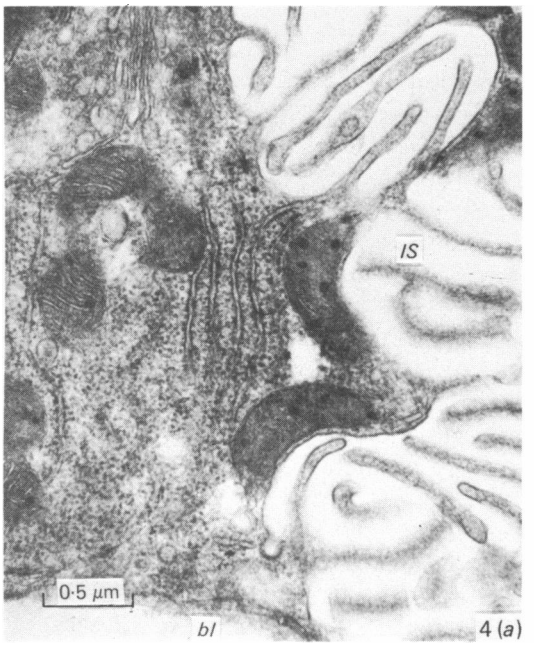
Fig. 4(*a–b*). Base of secretory cells of the ventral turbinate (Fig. 4*a*) and dorsal turbinate (Fig. 4*b*) glands. In both cases, the lateral borders of the cells carry long, thin processes which extend into the wide intercellular space (*IS*). Myoepithelial cells (*MY*) surround secretory alveoli and ducts of the dorsal turbinate glands inside the basal lamina (*bl*).

Fig. 5(*a–b*). Secretory cells (Fig. 5*a*) and duct cells (Fig. 5*b*) of the ventral septal glands. Secretory cells have extensive arrays of fine granular endoplasmic reticulum (*rer*), extensive Golgi membranes towards the lateral borders (*Gol*), and secretion droplets (*sd*) of variable density. Intercellular space (*IS*) is restricted towards the lumen (*L*) but more extensive towards the base of the cell. Duct cells have large vesicles of varying density which may be secretion droplets (*sd*). The cell base is smooth but there are extensive lateral cytoplasmic projections (arrows). *bl*, basal lamina.



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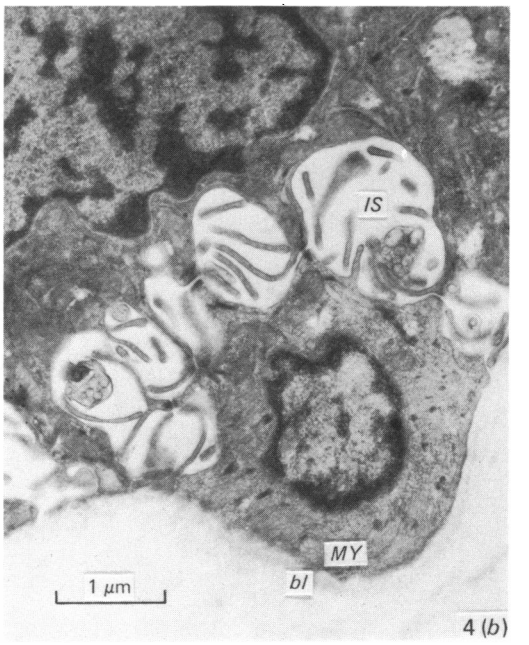

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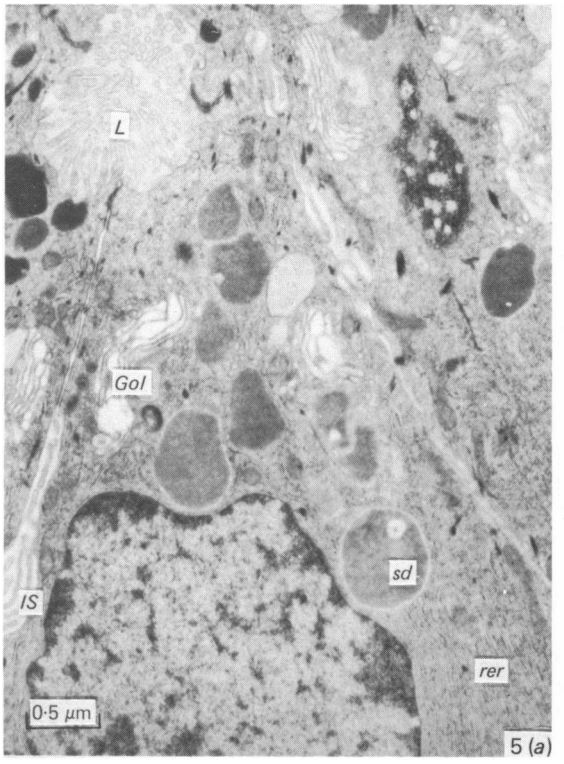

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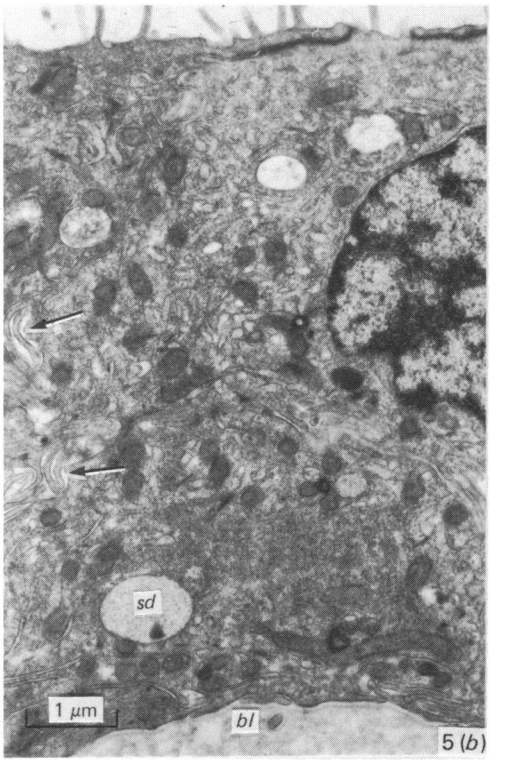

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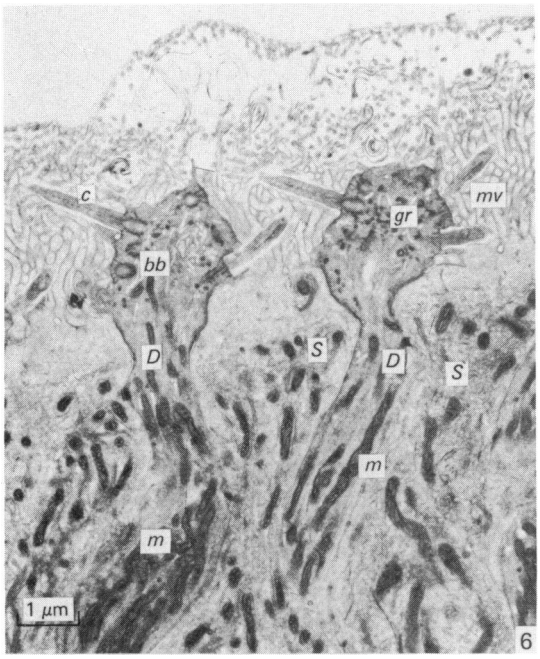


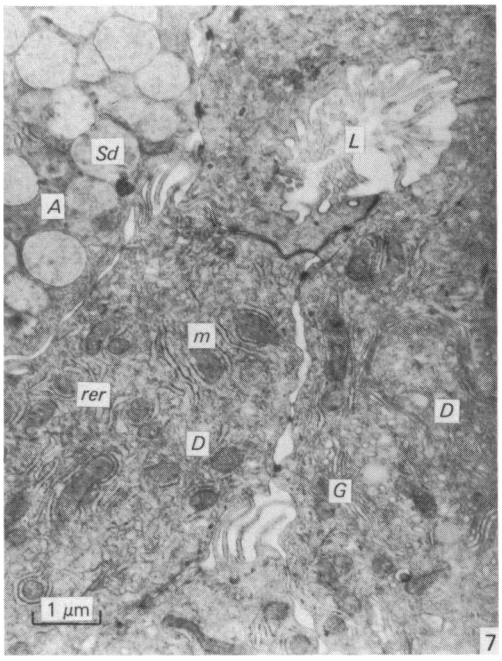


Fig. 6. Surface of the olfactory epithelium. Receptor cell dendrites (*D*) with long dark mitochondria (*m*) end in rounded olfactory rods bearing cilia (*c*). Rod cytoplasm contains dark granules (*gr*), vesicles and the ciliary basal bodies (*bb*). Supporting cells (*S*) provide a thick fringe of microvilli (*mv*) which enmesh the olfactory cilia. The surface cytoplasm of supporting cells is devoid of most organelles, but below this zone there are mitochondria and abundant parallel arrays of smooth endoplasmic reticulum.

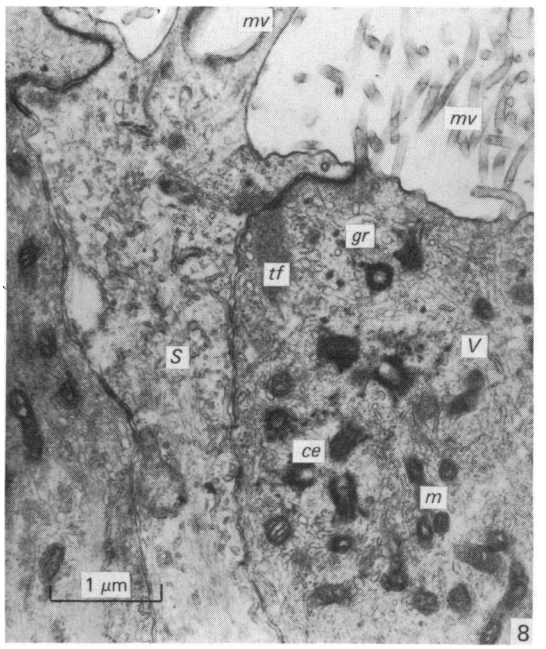
Fig. 7. Apical portion of secretory cells of Bowman's glands. Active cells (*A*) accumulate pale secretion droplets (*Sd*). Dark cells (*D*) have little or no evidence of secretion droplets, but have mitochondria (*m*) in close association with granular endoplasmic reticulum (*rer*) and Golgi apparatus (*G*) close to the lateral border. Microvilli project into the gland lumen (*L*).

Fig. 8. Surface of the vomeronasal sensory epithelium. The cytoplasm of a receptor cell (*V*) contains centrioles (*ce*), dark granules (*gr*) and mitochondria (*m*) and carries slender microvilli (*mv*). Supporting cells (*S*) have paler cytoplasm with tubular profiles of smooth endoplasmic reticulum. Microvilli (*mv*) are larger in diameter but less numerous, and more irregular than those on receptor cells. Bundles of tonofilaments (*tf*) are associated with surface cell junctions.

Fig. 9. Surface of non-sensory vomeronasal epithelium. Ciliated cells (*C*) have pale cytoplasm with dark mitochondria (*m*) and tubular stacks of smooth endoplasmic reticulum (*ser*). The cell surface carries microvilli (*mv*) as well as cilia (*c*). Non-ciliated cells (*NC*) have darker cytoplasm with cisternae of granular endoplasmic reticulum and scattered ribosomes. Surface microvilli resemble those on ciliated cells.

Fig. 10. Vomeronasal receptor cell nucleus (*VN*) and perikaryon, with Golgi apparatus (*Gol*), cisternae of rough endoplasmic reticulum (*rer*), scattered ribosomes and lysosomes (*Ly*). The paler cytoplasm of a supporting cell (*S*) and its nucleus (*SN*) can be seen on the right of the micrograph.

Fig. 11. Secretory cell of vomeronasal glands. Above the nucleus (*N*) the cytoplasm contains prominent Golgi (*Gol*), scattered ribosomes, and granular endoplasmic reticulum. Secretion droplets (*sd*) of dark but variable density accumulate towards the lumen (arrowed).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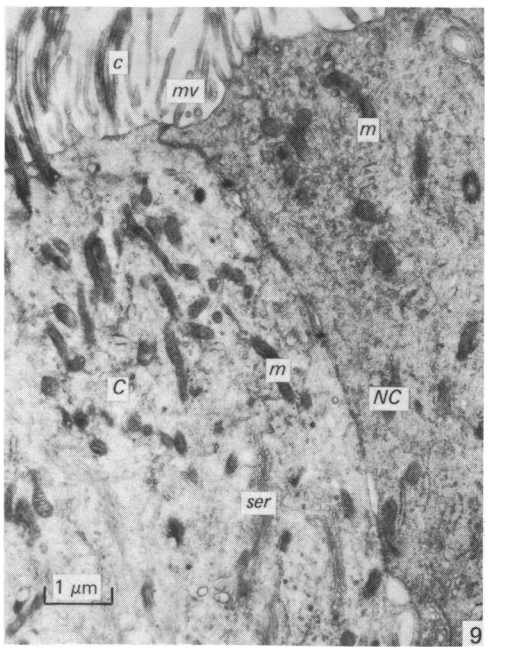
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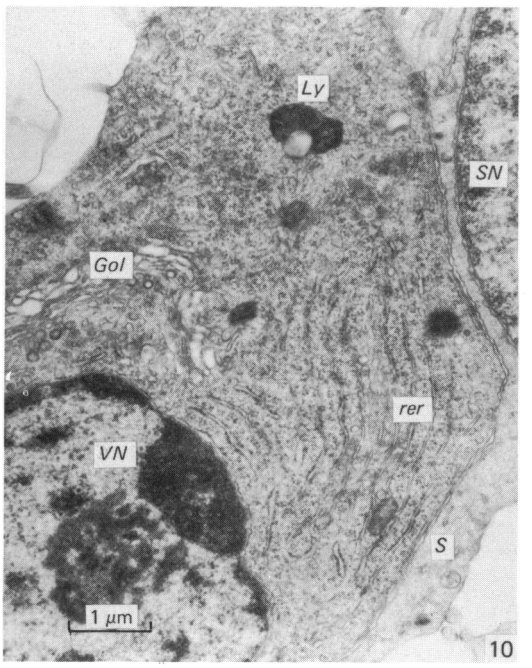
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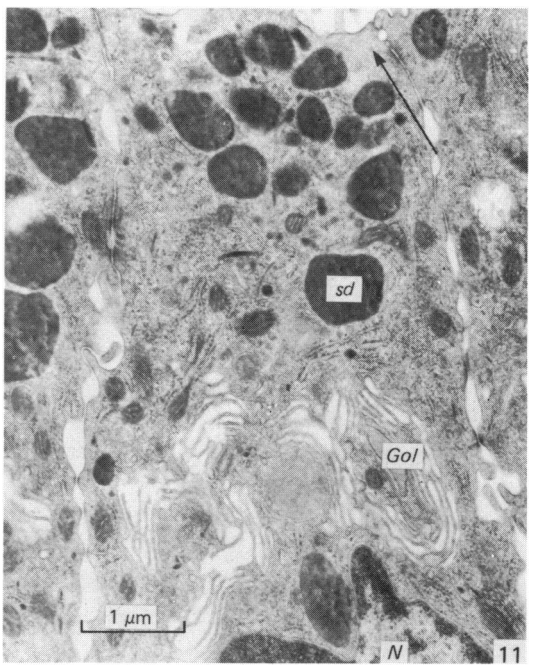
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11

their glands, these areas may provide adequate temperature and humidity control of the air reaching the olfactory membrane. Glandular duct organisation and the presence of myoepithelial cells provide a structural basis for modification of the composition and rate of delivery of secretions.

The histology of the nasal epithelium conforms to the general mammalian pattern. Respiratory epithelium of the koala varies in the frequency of goblet cells, though less so than in some marsupials where they are not present in sinus epithelium. Nerve endings at the base of the epithelium are most frequent rostroventrally around the opening of the incisive duct, and there is rich innervation under the squamous epithelium of the duct itself. Despite the differences in surface cells, the fine structure of basal cells appears to be identical in vestibular and respiratory epithelium.

Olfactory epithelium is not as extensive as in the possum, bandicoot, honey possum, and several macropod marsupials, and there is no separate septal olfactory organ. The vomeronasal organ is short; in the adult koala it is patent for about 10–12 mm, though its glands extend further along the base of the septum. The most direct access to the lumen of the organ is from the nasal cavity, but as the incisive duct opens just rostral to its own duct, odours from the mouth should reach the organ readily. The vomeronasal organ is reported to be important in sampling odours significant in mating (Wysocki, 1979). The flehmen grimace, which is considered to facilitate this sampling, has not been reported in the koala, but has been observed in the wombat (Gaughwin, 1979). Scent cues play a part in the social organisation of koalas since the male 'marks' trees with secretion from a sternal skin gland, and olfactory and vomeronasal systems seem to be involved in dietary selection. The koala will eat only the leaves of a limited range of eucalypt species, and even within a single species, individual trees are preferred to others (Robbins & Russell, 1978); sniffing precedes taste sampling in captive animals.

SUMMARY

The anatomy of the nose of the koala was studied from fixed 0·5 cm thick sections of a whole head. Right and left nasal cavities are separated by a slender septum which does not exhibit 'swell bodies'. Dorsal and ventral conchae are simple curved plates without elaborate scrolls; the ventral concha is recurved to form a bulla. The nasal cavity communicates with confluent rostral maxillary and frontal air sinuses. A ventrocaudal maxillary sinus opens from the ventral meatus close to the choanae. There is a frontal sinus dorsocaudal to the ethmoid region which does not communicate with the nasal cavity. Nasal and oral cavities communicate via incisive ducts, opening just rostral to the vomeronasal ducts. The vomeronasal organ extends from the level of the fourth incisor to the first cheek tooth.

The histology of the nasal area was examined by light and electron microscopy. Stratified squamous epithelium extends from the external nares to the incisive duct; nerve endings are frequent in association with its basal cells. Respiratory epithelium lines the nasal cavity proper, olfactory epithelium covers the ethmoturbinate bones, caudal dorsal concha and caudal septum, and sensory epithelium lines the medial aspect of the vomeronasal organ. Nasal secretions are provided by goblet cells and conchal and septal glands in respiratory areas, and by Bowman's and vomeronasal glands in the sensory areas. There are no lateral nasal glands, maxillary sinus glands or swell body glands.

I wish to thank Dr F. N. Carrick and Mr A. S. Brown for providing specimens for this study and Mr D. Bailey for drawing the diagrams. My thanks are also due to the staff of the Electron Microscope Department of the University of Queensland, and to the Wellcome Trust for a grant towards Electron Microscope facilities in the Department of Veterinary Anatomy.

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